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PART V, SECOND REVISION, CHAPTER 10: EVOLUTIONARY HISTORY

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The interpretation of evolutionary relationships is one of the most important aspects of modern biology and also connects biology and paleontology in the genealogical interpretation of extant and extinct organisms, combined in a unified biological system comparable to the family trees of humans. The taxonomical concept of Linnaeus (1735, 1758) combined organisms based on shared characters, as does modern cladistics (Hennig, 1950, 1965, 1989). Shared homologies or synapomorphies are used to understand evolutionary relationships, and early on, characters were often used in a kind of trial-and-error method before a better understanding of evolutionary connections was established. Clearly, the concentration on extant organisms can only produce an unfocused and biased view, but often this is all we have. The inclusion of the fossil record may provide much-needed additional information for evolutionary interpretation, and luckily some fossil material of the Hemichordata is available to help demonstrate the origin and early evolution of this group in the deep time of the early Paleozoic (Maletz, 2019).

Investigation of the evolutionary history of the Hemichordata based on the fossil record highlights the dilemma faced when combining extant and extinct groups of organisms. Bateson (1885) introduced the Hemichordata to science and suggested that they were closely related to the Chordata due to the presence of a notochord, the precursor of the backbone of the vertebrates. The Hemichordata are now regarded as a sister group to the Echinodermata, and some of the early interpretations have been revised considerably (e.g., Halanych, 1995; Cannon & others, 2009; Philippe & others, 2011; Maletz, 2014). The Enteropneusta is a group with an extremely poor fossil record. Only in recent years has it been possible to relate a few of the fossil enteropneusts to the four extant families (Cameron, 2016, 2018). A stem-group taxon found in the Burgess Shale of British Columbia apparently produced a possible housing construction (Nanglu & others, 2016) that has been linked to the pterobranch tubarium formation. However, the crown group Enteropneusta has been verified only from the late Paleozoic onward; and except for five taxa, all known species are extant.

Due to the lack of information on the Enteropneusta, the discussion on the evolutionary history of the Hemichordata will here be focused on the Pterobranchia. The pterobranch tubaria form extremely important fossil remains for geological research and render them ideal for evolutionary studies. However, these housing constructions provide only a limited insight into the evolutionary history of the clade. The soft-bodied zooids did not leave an interpretable fossil record, and we do not know how much evolutionary change has been involved in the organization of these animals since their first fossil appearance during the early Palaeozoic. It is unknown when and how the pterobranchs started to develop their typical clonal reproduction method and why they became the leading planktic organisms in the

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early Palaeozoic but then largely disappeared during the late Paleozoic.

Because graptolites (fossil Pterobranchia) are thought to be common and widely distributed, it may be reasonable to assume that their evolutionary history is well known. However, only the general picture is outlined from the fossil record, and numerous questions still remain. The story began with the origin of this fascinating group of organisms probably somewhere during the early Cambrian time interval and led to the few members that are still around today.

EVOLUTIONARY INTERPRETATIONS

The differences in the tubarium construction have been used to interpret evolutionary relationships of the graptolites, and early discussions go back to NICHOLSON and MARR (1895) and ELLES (1898), who were clearly aware of the polyphyletic concept of many of the established genera at their time. They understood that many characters used to define taxa evolved independently in unrelated lineages, even though they did not yet use the term convergent evolution as did LENZ and MELCHIN (2008) when comparing the Silurian monograptids *Cochlograptus* OBUT, 1987 and *Testograptus* PŘIBYL, 1967. However, NICHOLSON (1868) had already discussed the zoological position of the graptolites and looked for homologous characters to connect the group with other organisms.

ELLES (1922, p. 174) discussed proximal end development types and a number of trends leading to her “lines of evolution in the Graptoloidea,” which, again provides a fairly simplified concept. A later version of this discussion appeared in JAEGER(1978). It was also clear to him that the evolution of the graptolites was based on numerous lineages with parallel and convergent evolution due to the constructional limitation of the bausteine [building blocks] of their tubaria. JAEGER discussed eight trends in the evolution of the graptolites and stated (JAEGER, 1978, p. 8), that “Diese Trends wirken gleichzeitig nebeneinander oder abwechselnd und nacheinander; sie sind miteinander korreliert oder voneinander unabhängig. Sie sind nicht gleichwertig. Die Reihenfolge ihrer Behandlung ergibt sich aus Zweckmässigkeitsgründen der Darstellung. Diese ist kein Kriterium für die Wertigkeit des einzelnen Trends.” [These trends act simultaneously and parallel to each other, or after one another. They are not equal. Herein, the succession in their discussion is based on practicality of the demonstration. It does not provide a criterion for the value of the individual trends.]

Thus, patterns of parallel and convergent evolution appear to be a fundamental feature in the evolution of the Graptolithina, implied by the constructional limitations of a tubarium formed from fusellar half rings as branching tubes (see MALETZ, 2017a, p. 121). Graptolite evolution can thus be regarded as strongly directional (see MITCHELL, 1990).

A large number of studies discuss various aspects of graptolite evolution (e.g., URBANEK, 1966, 1970, 1987; RICKARDS, 1977; KOREN’ & SUJARKOVA, 2004; URBANEK & others, 2012; and many others), often focusing on individual, short-lived anagenetic lineages, typically expressed by the example of the evolution of the *Demirastrites triangulatus* group (SUDBURY, 1958; ŠTORCH & MELCHIN, 2019) and rarely considering a larger picture (see RICKARDS, HUTT, & BERRY, 1977; MITCHELL, 1990; FORTEY & COOPER, 1986; MITCHELL & others, 2013; CRAMPTON & others, 2016, 2018). These individual studies provide puzzle pieces of important information, and fitted together give us an idea on the way evolution through time modified the tubaria of the graptolites.

BULMAN (1958), in a classic study, revised the ideas of ELLES (1922) and defined a sequence of four overlapping subfaunas (Fig. 1). These were based on some major characteristics. The anisograptid, dichograptid, diplograptid, and monograptid faunas can easily be recognized by their typical tubarium shapes. However, other tubarium developments of these faunas render differentiation difficult at a closer view. Even in

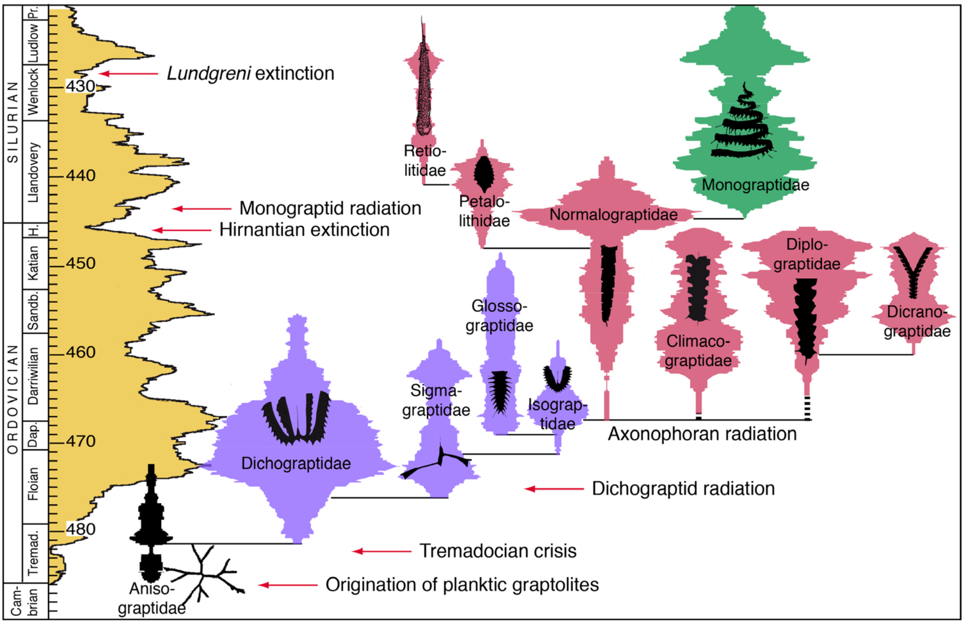

FIG. 1. Graptoloid diversity and the main groups of graptoloids. The anisograptid (*black*), dichograptid (*purple*), diplograptid (*red*), and monograptid (*green*) faunas can easily be recognized (based on data in Sadler, Cooper, & Melchin, 2011; adapted from Maletz, 2017b, fig. 9). Note: Only some of the events in graptoloid history are marked on the diagram. Pr = Pridoli; H = Hirnantian; Sandb = Sandbian; Da. = Dapingian; Tremad = Tremadocian.

the most recent interpretations of graptolite diversity and evolution (see Sadler, Cooper, & Melchin, 2011; Cooper & others, 2014), these four subfaunas are recognizable and have been defined in a seemingly identical way as high-level taxonomic units (Fig. 1). However, Elles (1922), Bulman (1933, 1958) and Jaeger (1978) understood these groups as grades of organization that are progressively replaced as the various lineages evolve nearly parallel to each other through time. Modern cladistic interpretations see the patterns as a number of independently evolving clades, but the general picture remains the same.

Detailed information on the evolution of benthic graptolite faunas is not available. Thus, they do not appear in any diversity studies of graptolites. Bouček (1957, fig. 75) and Chapman, Durman, and Rickards (1996) provided some suggestions on the basic evolutionary relationships of the dendroid graptolites. Andres (1977, 1980) compared the fusellar construction of Ordovician graptolites and extant pterobranchs and concluded a possible closer relationship of these two groups. Mitchell and others (2013), in a cladistic analysis, included the modern pterobranchs in their concept of the graptolites but did not analyze the various groups of the dendroids in detail.

More recently, cladistic methods were used to interpret graptolite taxonomy and evolution and to attain information on origination and extinction events that may have shaped the evolutionary history of the group (e.g., Fortey & Cooper, 1986; Mitchell, 1987; Melchin, 1998; Fortey, Zhang, & Mellish, 2005; Maletz, Carlucci, & Mitchell, 2009; Melchin & others, 2011; Mitchell & others, 2013; Melchin, Lenz, & Kozłowska, 2017). These cladistic analyses support the main taxonomical concepts of the Graptolithina but cover only some of the recognized clades. A stratocladistic attempt to provide a better understanding of graptolite evolution of a number of Silurian monograptid taxa indicated the need for more detailed morphological investigation for support (Wittingham, Radzevičius, & Spiridonov, 2020).

Sadler, Cooper, and Melchin (2011) noted that the tempo of evolutionary change may have been slower during the Ordovician and faster during the Silurian. Clearly the data indicate an interconnection to climatic changes; and during colder periods, extinction events may have reduced the diversity of the graptoloids considerably by influencing the equatorial or warm water faunas more strongly. Over time, a general understanding of graptolite evolution has been achieved from the origin of the planktonic graptoloids near the base of the Ordovician to their final extinction during the early Devonian. However, major gaps still exist in the evolutionary understanding of the benthic groups, as their fossil record is relatively poor and incomplete.

ORIGINATION, EXTINCTION, AND DIVERSITY

The macroevolutionary trends in this directional evolution of graptolites have been the focus of diversity studies, indicating a number of extinction, origination, and diversification intervals during the Paleozoic (Fig. 1). A considerable number of extinction events have been established for the graptoloid clade (e.g., Štorch, 1995; Sadler, Cooper, & Melchin, 2011; Bapst & others, 2012; Maletz, 2017a), leading to its near extinction and also to distinct episodes of radiation after a particular extinction event. Various extrinsic factors have been connected to the evolutionary rates of the Ordovician and Silurian planktic graptolites, including climatic conditions and even Milankovitch cycles (Cooper & others, 2014; Crampton & others, 2016, 2018, 2020). Because graptolites are most commonly preserved in black shales, these lithological intervals may have led to an overinterpretation of graptolite diversity due to the better preservation of the specimens in anoxic environments (Maletz, 2018, 2020a). Graptolites are poorly represented in other sediment types and these faunas are underrepresented, an aspect in graptolite diversity in need of further investigation.

Quantitative methods have recently been employed to understand biostratigraphic distributions and interpret evolutionary relationships and events in the geological history of the graptolites. Foote and others (2019) discussed the completeness of the graptoloid record based on a mathematical model, and Crampton and others (2020) discussed the possibility of sampling bias for the macroevolutionary interpretation of graptolite evolution. Even though sampling is a major factor in the interpretation (see also Boyle & others, 2017), a connection to the sediment type and graptolite taphonomy has rarely been made (Maletz, 2020a).

The Hirnantian event close to the end of the Ordovician (Fig. 2) was one of the largest and best investigated events in graptoloid history (Koren', 1979, 1991; Chen & others, 2003, Chen, Fan, & others, 2005; Štorch & others, 2011). Chen, Melchin, and others (2005) and Finnegan and others (2011) describe the event as a two-step extinction starting with the first step near the Katian/Hirnantian boundary and a second one at the end of the Hirnantian. Also, Bapst and others (2012) discussed two separate extinction episodes during the Hirnantian, associated with the initiation and termination of a global cooling period, located at the base and the top of the Hirnantian interval. Bond and Grasby (2020) recently suggested an early cooling phase and a second phase of warming and anoxia development for the Hirnantian mass extinction, which supports this idea.

During the Hirnantian extinction event, most warm water graptolite faunas were severely affected, and the Diplograptina went extinct in the second phase, while at the same time, the Neograptina experienced an enormous radiation, suggesting the demise of most warm-water faunal elements (Melchin & Mitchell, 1991; Štorch & others, 2011; Bapst & others, 2012).

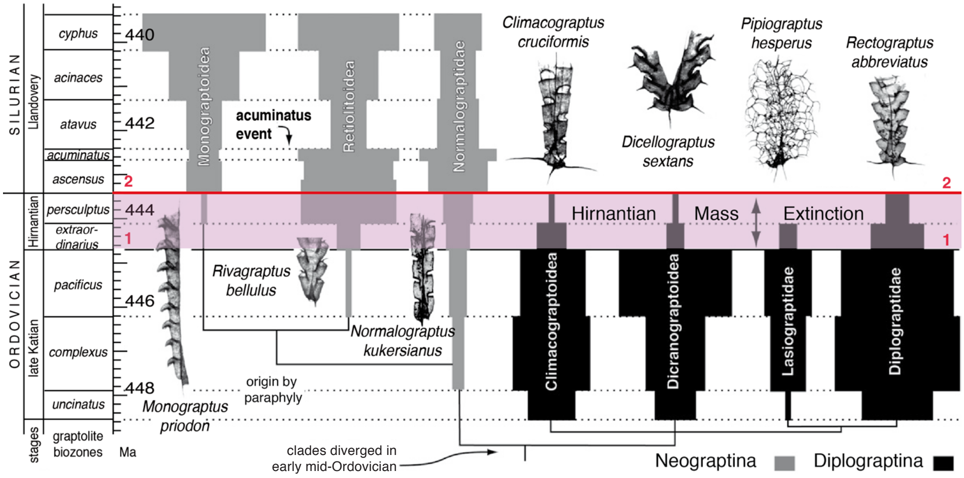

Fig. 2. Interpretation of the Hirnantian extinction and replacement of the Diplograptina (*black*) by the Neograptina (*gray*) (adapted from Bapst & others, 2012, fig. 1).

A distinct replacement of the Diplograptina faunas by the Neograptina faunas can be demonstrated (Fig. 2). Sadler, Cooper, and Melchin (2011, fig. 13) showed a diversity of less than 20 species during the Ka4-Hirnantian crisis (circa *Metabolograptus persculptus* Biozone?), but Bapst and others (2012) indicated about 25 species in the *Metabolograptus persculptus* Biozone. Goldman and others (2011) listed 39 species of normalograptids from the *Metabolograptus persculptus* Biozone alone (his zone 13, Bo5), but the list does not include the diplograptine faunal elements.

Štorch and others (2011, fig. 3) regarded a number of the Hirnantian Diplograptina as Lazarus taxa—taxa showing an apparent extinction but reappearing later on. As the authors indicated the ranges of these taxa through the supposed extinction interval, the record would not represent a real extinction, and the diversity in the extinction interval may be considerably exaggerated. The faunal change may better be interpreted as a turnover and successive replacement that does not need to be connected to an intense extinction event, as in the *Lundgreni* Event (Koren’, 1987; Jaeger, 1991) in which the diversity of graptolites was extremely reduced. Still, the selectivity of the event suggests that certain graptolite groups were more vulnerable to extinction than others. Crampton and others (2016, p. 1498) suggested that “old species were selectively removed” during the Late Ordovician mass extinction, but Sheets and others (2016, p. 8380) recognized a “preferential decline in abundance of dysaerobic zone specialist species.” The high diversity in the *Metabolograptus persculptus* Biozone could also be based on the increased international attention of the interval due to its being defined as a Global Stratotype Section and Point (GSSP) at the base of the Silurian and the supposed extinction interval in the Hirnantian. This attention led to an extreme splitting of specimens into numerous local graptolite species (Sobolevskaya, 1974; Chen & Lin, 1978; Ni, 1978; Mu & Ni, 1983; Fang & others, 1990; Legrand, 2001, 2009; Mu & others, 1993; Chen, Fan, & others, 2005; Chen & others 2007, 2020), possibly masking the real impact of the event on graptolite diversity. However, this suggestion should not downplay the real extinction event that can be recognized in the Late Ordovician and is not restricted to the graptolites.

The term Lazarus effect (see Flessa & Jablonski, 1983; Wignall & Benton, 1999) has been used to describe the cryptic appearance of members of lineages disappearing at an extinction event and reappearing later on (Urbanek, 1993, 1998; Rickards & Wright, 2002; Štorch & others, 2011), which should not be confused with a genuine extinction. Adding these species to the diversity diagram (Štorch & others, 2011, fig. 5) would lead to a somewhat different interpretation: very few species of the Diplograptina fauna went extinct at the base of the *Metabolograptus extraordinarius* Biozone.

The reappearance of species of the genus *Cyrtograptus* Carruthers in Murchison, 1867 as relic elements in the Ludlow of New South Wales (Rickards & others, 1995) could be interpreted as a Lazarus effect. Alternately, they may be based on parallel evolution of main tubarium features, thus needs reinvestigation. This reappearance may not represent a genuine record of the genus *Cyrtograptus,* but the emergence of the genus *Formosograptus* Bouček, Mihajlovic, & Vaselinovic, 1976, generally lacking cladia (see Urbanek, 1997).

The largest extinction event influencing graptolite evolution may have been the Silurian *Lundgreni* Event (e.g., Koren', 1987; Lenz & others, 2006; Crampton & others, 2016) or the Great Crisis of Jaeger (1991) during the early Homerian (Wenlock) (see Fig. 1). During this event, nearly all monograptids and retiolitids disappeared, and the two groups rediversified after a short interval in which only two graptoloid taxa, *Pristiograptus* Eisel, 1912 and *Gothograptus* Frech, 1897, have been recognized as the sole survivors of the previously dominating Silurian neograptine and monograptid clades. Urbanek (1997, 1998) identified this bottleneck effect of near extinction or survival and recovery with the term oligophyly.

Cooper and others (2014) suggested different causal linkages for the graptolite diversity patterns in the Ordovician and Silurian. They postulated relatively stable marine environments for the Ordovician, but the Silurian appeared to be characterized by more volatile climatic changes leading to a number of distinct extinction events. Cooper and Sadler (2010) discussed the extinction risk of graptolite faunas and came to the conclusion that the facies preference of graptolites predicted their extinction risk. They suggested that species restricted to the deep-water classical graptolite facies (deep-water black shales) show a distinctly lower mean duration than faunal elements also found in shallow-water or platform regions. The analysis, however, does not include the notion that the anoxic black shale facies favors preservation of organic material and thus, superior preservation of graptolite tubaria.

EVOLUTIONARY TRENDS

Evolutionary studies of graptolites can be used to differentiate micro- and macroevolutionary patterns, but the differentiation is not easy, as the fossil record is typically quite patchy, and micro-evolutionary steps may be nearly impossible to trace. Tracing the change of single species into a different, derived species may be termed micro-evolution. This is exemplified by the work of Sudbury (1958) and Štorch and Melchin (2019), who demonstrated anagenetic change in the genus *Demirastrites* Eisel, 1912. They documented the stepwise generation of changes in faunal populations until differences became large enough to indicate a speciation event. Numerous further examples can be found in the scientific literature (see an overview for Silurian monograptids in Rickards, Hutt, & Berry, 1977).

Urbanek (1995) discussed the *Wolynograptus spineus* lineage in some detail from chemically isolated material and was able to trace anagenetic changes in the construction of the thecal apertures through a number of species. *Wolynograptus acer* Tsegelnjuk, 1976 evolved through the apertural addition of new characters to the intermediate *Wolynograptus protospineus* (Urbanek, 1995) and finally to *Wolynograptus spineus* (Tsegelnjuk, 1976) (Fig. 3). The paired apertural spines of *Wolynograptus spineus* are reminiscent of

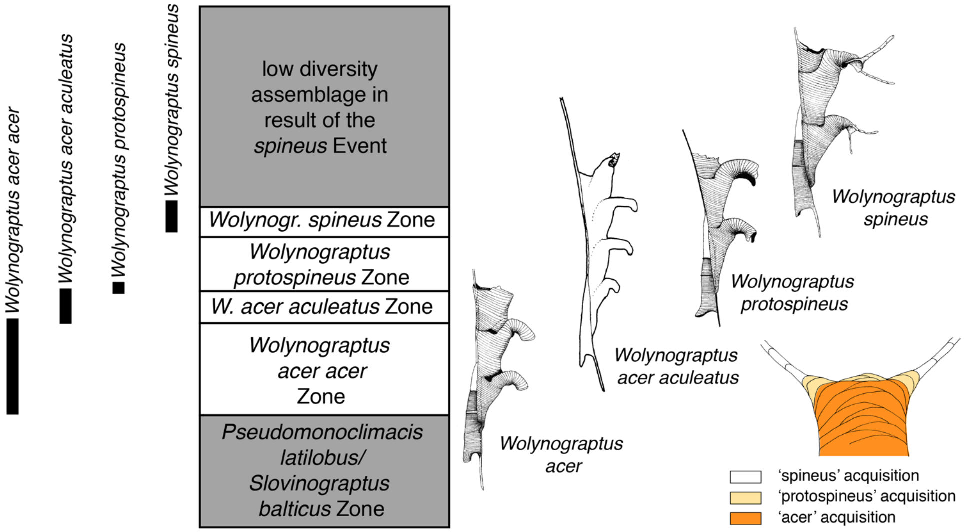

FIG. 3. Phyletic evolution in the *Wolynograptus spineus* (TSEGELNJUK, 1976) lineage based on URBANEK (1995) (adapted from Maletz, 2017a, fig. 7.7).

the much older *Monograptus priodon* group, but the species cannot be identified as a cryptogenic faunal element or interpreted as a Lazarus taxon. It was a newly evolved taxon with a homoplastic character indicative of parallel or convergent evolution. Thus, tracing the micro-evolutionary changes in a single lineage was used to understand macroevolution in monograptids and to determine characters as homoplastic and not homologous.

DIRECTIONAL EVOLUTION AND HOMOPLASY

Larger-scale differentiations or macroevolutionary patterns occurred in the evolution of groups such as the Dichograptina, Axonophora, or Neograptina, and eventually the Monograptidae, and correspond to the trends in graptolite evolution as suggested by ELLES (1922). These trends have invariably been understood as polyphyletic and not strictly interpretable in a phylogenetic way.

Due to the constructional limitations imposed by the formation of thecal tubes by fusellar half rings, "many tubarium features evolved again and again independently during the evolutionary history of the graptolites" (MALETZ, 2017a, p. 121), a factor identified as directional evolution and discussed for Ordovician axonophorans by MITCHELL (1990). Numerous characters of graptolite colonies cannot be used to simply postulate phylogenetic relationships and explain evolutionary lineages. These characters have to be interpreted as homoplastic, and morphological similarities are based on convergent evolution (see LANKESTER, 1870). Thus, real homologies are difficult to detect in graptolites, and a detailed morphological analysis is needed to trace them (Fig. 4).

Excellent examples of this directional evolution and convergence can be seen in a large number of groups (MITCHELL, 1990). The decrease of the number of stipes was regarded as of prime importance initially, but NICHOLSON and MARR (1895, p. 531) had already stated, that "the number of stipes in the polypary is a character of minor importance." Thus, translated into modern terms, the number of stipes is not a homologous character (Fig. 4.1–4.2). This statement may be supported by the modern inclusion of single-stiped tubaria into several unrelated clades (e.g. *Azygograptus* NICHOLSON & LAPWORTH in NICHOLSON, 1875 in Sigmagraptidae; *Nicholsonograptus*

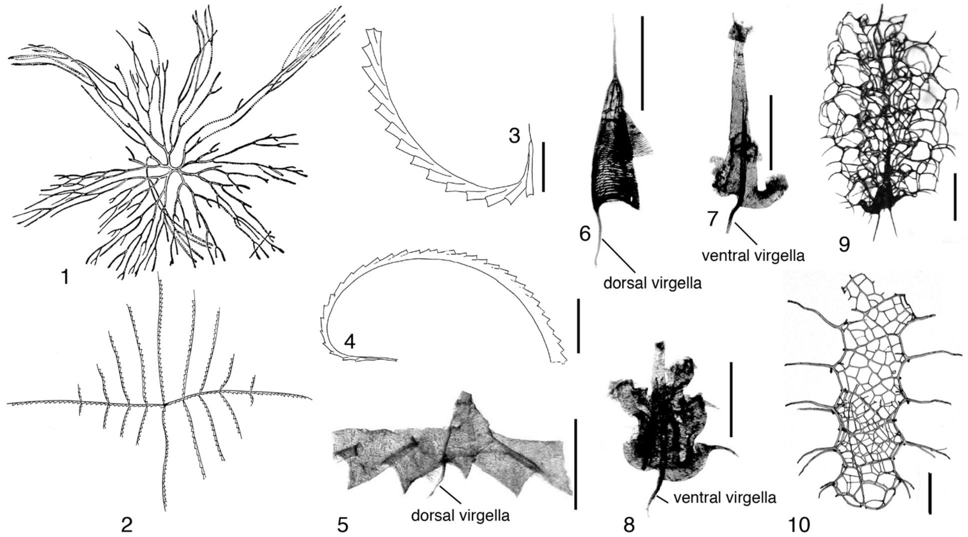

Fig. 4. Examples of directional evolution and homoplasy. *1*, *Clonograptus flexilis* (Hall, 1865), multiramous tubarium with dichotomous branching (Hall, 1865, fig. 8); *2*, *Abiesgraptus multiramosus* Hundt, 1935, multiramous tubarium with cladial branching (adapted from Jaeger, 1959, fig. 25); *3*, *Cymatograptus validus* (Törnquist, 1904), strongly curved taxon with single stipe (reconstructed from Beckly & Maletz, 1991, fig. 19B); *4*, *Coronograptus cyphus* (Lapworth, 1876), strongly curved single stiped monograptid (reconstructed from Zalasiewicz, Williams, & Akhurst, 2003, fig. 2A); *5*, *Xiphograptus lofuensis* (Lee, 1961), showing dorsal virgella (Maletz, 2010a, fig. 8C); *6*, *Phyllograptus typus* Hall, 1865, dorsal virgella (Maletz, 2010a, fig. 6C); *7–8*, *Levisograptus sinicus*, ventral virgella (Maletz, 2010a, fig. 5); *9*, *Pipiograptus* sp. showing meshwork of external bars (Maletz, 2017a, fig. 11.8J); *10*, *Spinograptus spinosus* (Wood, 1900), retiolitid graptolite with meshwork of ancora sleeve (Maletz, 2010b, fig. 5A). *1, 3, 5–8:* Ordovician; *2:* Devonian; *4, 9–10:* Silurian. Scale bars, 1 mm, with the exception of *4,* which is 5 mm.

Bouček & Přibyl, 1952 in Sinograptidae; Monograptidae as a Silurian clade). Maletz (2017a, fig. 7.6) illustrated the situation as a prime example of convergent evolution (Fig. 4.3–4.4). It is also supported by the recognition of cladia forming secondarily multiramous tubaria (Fig. 4.1–4.2) in various clades of the Graptolithina. As we now know, cladia evolved independently in the Pterograptidae (Skwarko, 1974; Maletz, 1994), the Dicranograptidae (Maletz, 2020b), the Nemagraptinae (Finney, 1985), and in a number of monograptid genera (Strachan, 1952; Urbanek, 1963).

The repeated origination of retiolitid-type developments in the graptolites may be one of the most stunning and easily recognizable examples of convergent evolution. The retiolitid-type development is characterized by the independent extrathecal development of a meshwork of lists as in the Ordovician Lasiograptidae (Fig. 4.9) and especially in the Silurian Retiolitidae (Fig. 4.10), in which the precise development shows a very different origin of comparable features (Lenz & others, 2018).

Another prime example of directional and convergent evolution involves the formation of the virgella spine (Fig. 4.5–4.8), initially regarded as a character used to define the Virgellina as a monophyletic group (Fortey & Cooper, 1986). At least three instances of independent origin and evolution of a virgellar spine have been identified, and Maletz (2010a) differentiated a dorsal and a ventral virgellar spine in the Graptolithina. The loss of bithecae in the late Tremadocian appeared even more complex than expected to Fortey and Cooper (1986). A polyphyletic loss of the bithecae has been suggested by a number of authors (Bulman, 1960; Erdtmann, 1982; Lindholm, 1991) and can be supported by the presence of at least a sicular bitheca in the sigmagraptine

Paradelograptus (Maletz, Zhang, & Vandenberg, 2018).

Numerous further characters may be identified as independently evolved in widely separate clades, making cladistic interpretations difficult without the detailed morphological knowledge of the tubarium construction of the graptolites. The instances of homoplasy in the Pterobranchia discussed here can also be described in the terms of convergence and parallel evolution in various graptolite groups.

Rigby and Milsom (1996) suggested neoteny or paedomorphosis as the motor for the evolution of planktic graptolites. It is, however, difficult to use the concept for the development of the colonial astogeny of the graptolite colonies or in fact, for colonial organisms in general. Rickards (1977) discussed a number of cases that may indicate paedomorphosis, including the evolutionary change from *Petalolithus* Suess, 1851 to *Cephalograptus* Hopkinson, 1869. In this example, Rickards (1977) interpreted the elongation and reduction of the number of thecae in the tubarium as a possible example of neoteny. There is no change in the size and development of the sicula in these forms. He also regarded the Ordovician genus *Corynoides* Nicholson, 1867 as a possible paedomorphic derivative of the isograptids, achieved through the loss of the unrestricted growth of the graptolite colony.

In the Dichograptina, the first few thecal pairs are typically fairly slender as are the stipes. Through the astogeny, the stipes widen considerably distally as in *Tetragraptus* Salter, 1863 or in *Didymograptellus* Cooper & Fortey, 1982 (see Williams & Stevens, 1988, fig. 44) but also in many other taxa. This can be regarded as a simple expression of morphological gradients in graptolite colonies, even though changes in thecal construction are minimal. Morphological gradients are most commonly described from Silurian monograptids (e.g., Bulman, 1958; Hutt, 1974) and are often easily visible even in flattened shale material. Maletz and others (2019) described the dramatic change of the thecal style in *Paramonoclimacis sidjachenkoi* Obut & Sobolevskaya in Obut, Sobolevskaya, & Bondarev, 1965 from chemically isolated material (Fig. 5). The proximal thecae of this taxon bear strongly coiled thecae with a streptograptid nozzle (Fig. 5.3–5.4), changing distally to dorsal hooks associated with two lateral lobes (Fig. 5.8) through a number of intermediate thecal stages (Fig. 5.5–5.7). Similar thecal gradients can be seen in genera such as *Torquigraptus* Loydell, 1993, *Pernerograptus* Přibyl, 1941, *Pribylograptus* Obut & Sobolevskaya, 1966, and to a lesser degree in *Coronograptus* Obut & Sobolevskaya in Obut, Soboleveskaya, & Merkureva, 1968 (Hutt, 1974; Lukasik & Melchin, 1997).

Bulman (1958) and Urbanek (1960) discussed and illustrated thecal gradients of a number of examples of Silurian monograptids. They explained the development of *Cyrtograptus* in which cladial branches show initial thecae that are quite different from the thecae of the main stipe at which the cladium is developed but can be compared to much more distal thecae (Fig. 6). In this example, a thecal gradient is combined with cladial branching, allowing recognition of the exact point in time of initiation of the growth of the cladial branch. They interpreted a delay in the initiation of the growth of cladial branches following the suggestion of Thorsteinsson (1955), who first described this delay in *Cyrtograptus perneri* Bouček, 1933 (see revision of taxon in Lenz & others, 2012, p. 32). However, Bulman (1958) and Urbanek (1960) illustrated a specimen of *Cyrtograptus murchisoni* Carruthers in Murchison, 1867 as an example in which the thecal gradient has not yet been described in detail (Fig. 6.1). Information of the thecal differentiation can be taken from other taxa of the genus (Fig. 6.2–6.4). The phenomenon was called retardation and was explained by the observation, that "before the first signs of the growth of the first cladial theca, some 3–4 next thecae have appeared on the main stipe" (Urbanek, 1960, p. 158). Urbanek (1963, p. 230)

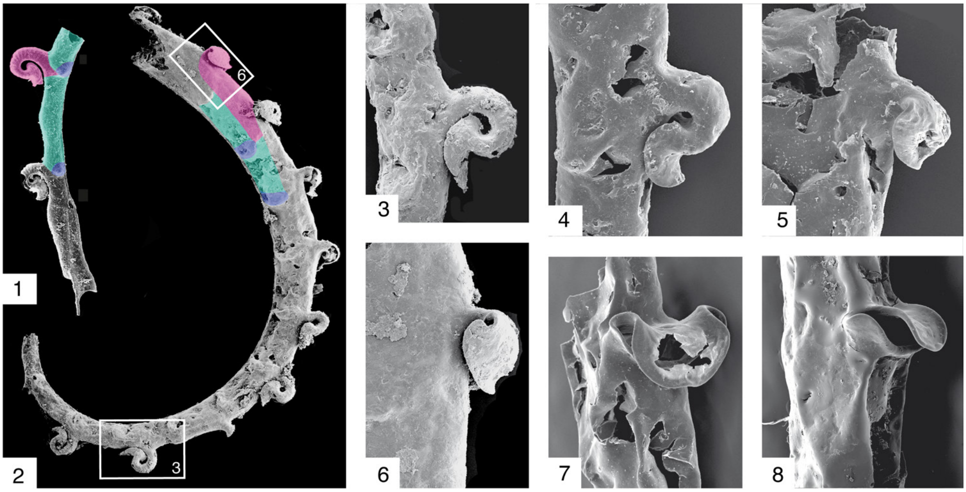

FIG. 5. *Paramonoclimacis sidjachenkoi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA & BONDAREV, 1965) showing thecal gradients. *1*, proximal end with two thecae; *2*, strongly curved proximal fragment lacking sicula; *3–4*, proximal thecae; *5–6*, median thecae with wide hood; *7*, thecal hood reduced in width; *8*, slender thecal hood and lateral lobes of distal theca (new; details of specimens in MALETZ & others, 2019). Not to scale.

suggested that this delay may be described by the "law of morphological equivalence of simultaneously budding thecae, established by THORSTEINSSON (1955)." The "distribution of suitable morphogenetic substances" produced by the oozoid (siculozooid) may be the mechanism behind this delay and lead to the different thecal styles (URBANEK, 1963, p. 230). It could also help to understand bipolar stipes as the regeneration of stipe fragments, in which the theca growing to one side is often different in size and shape to the one on the other side. Oldest bipolar tubaria without the presence of a sicula were recognized in the Middle Ordovician and described as *Janograptus* TULLBERG, 1880, but are more common in Silurian monograptids (see RICKARDS, HUTT, & BERRY, 1977). ALBANI and others (2001) illustrated a Darriwilian (Middle Ordovician) janograptid specimen with the first thecal apertures on the two stipes of the bipolar tubarium distinctly different in size. JAANUSSON (1973) discussed morphological discontinuities in the evolution of graptolites and the possible presence of polymorphic populations. He suggested that this was commonly involved in the change of number of stipes in graptolite colonies and provided a number of examples, including the three- and four-stiped specimens of *Tshallograptus fruticosus* (HALL, 1858) (see VANDENBERG, 2017, for a modern taxonomic approach). He expected that, in these cases, both morphological types would coexist for some time as genetic polymorphs. SKEVINGTON (1966, 1967) elaborated on the concept of genetic polymorphism in the case of *Holmograptus* KOZŁOWSKI, 1954 and *Nicholsonograptus*, suggesting that both were likely to be intraspecific variants of a single species. However, both genera are now regarded as separate members of the Sinograptidae (MALETZ, ZHANG, & VANDENBERG, 2018) and the concept of evolutionary change through polymorphy has not been proven for graptolites.

Biogeography was also involved in the evolutionary differentiation of graptolite faunas and was important for the formation of biogeographically distinct regions. See Chapter 8: Paleogeography of the Hemichordata, *Treatise Online* (MALETZ 2020c).

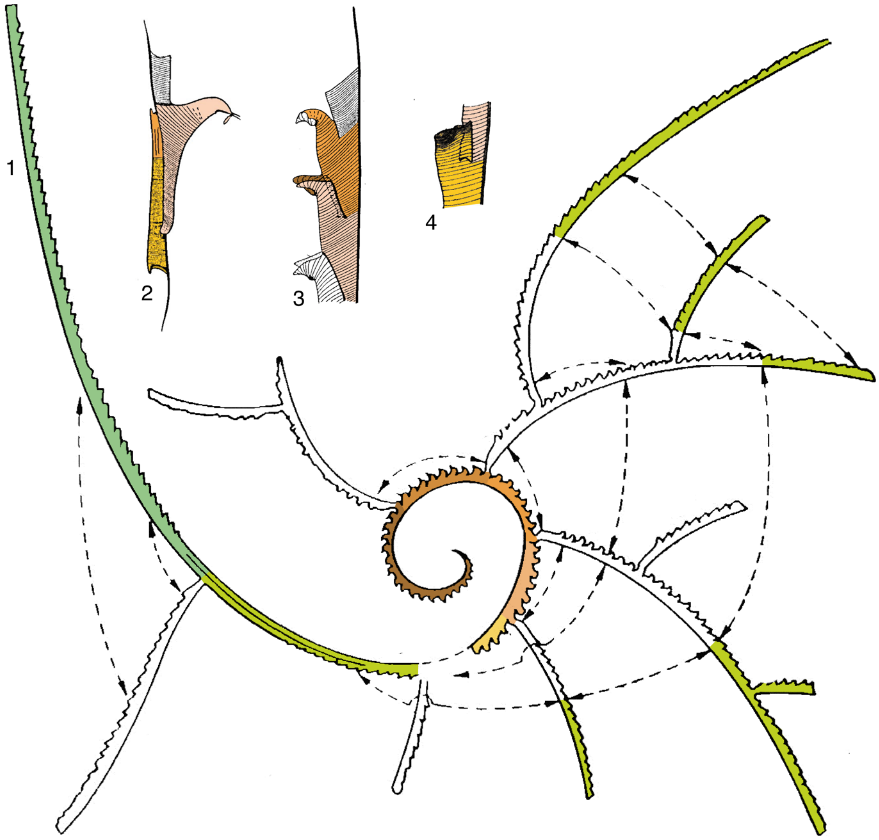

FIG. 6. Thecal gradients in cladial stipes. *1, Cyrtograptus murchisoni* CARRUTHERS, 1867 (new; based on Bulman, 1958, fig. 7 and URBANEK, 1960, fig. 10); *2–3, Cyrtograptus perneri* BOUČEK, 1933, proximal end and thecae from median part of colony (adapted from Thorsteinsson, 1955, fig. 1–2); *4, Cyrtograptus hamatus* (BAILY, 1862), distal theca (Teller, 1976, fig. 12). Illustrations not to scale.

REFERENCES

Albani, Roberto, Gabriella Bagnoli, Jörg Maletz, & Svend Stouge. 2001. Integrated chitinozoan, conodont and graptolite biostratigraphy from the Upper Cape Cormorant Formation (Middle Ordovician), western Newfoundland. Canadian Journal of Earth Sciences 38:387–409.

Andres, Dietmar. 1977. Graptolithen aus ordovizischen Geschieben und die frühe Stammesgeschichte der Graptolithen. Paläontologische Zeitschrift 51 (1/2):52–93.

Andres, Dietmar. 1980. Feinstrukturen und Verwandtschaftsbeziehungen der Graptolithen. Paläontologische Zeitschrift 54(1/2):129–170.

Baily, W. H. 1862. Graptolites from Co. Meath. Journal of the Geological Society of Dublin 9:300–306.

Bapst, D. W., P. C. Bullock, M. J. Melchin, H. D. Sheets, & C. E. Mitchell. 2012. Graptoloid diversity and disparity became decoupled during the Ordovician mass extinction. Proceedings of the National Acadeny of Sciences 109(9):3428–3433.

Bateson, William. 1885. Note on the later stages in the development of *Balanoglossus kowalevskii* (Agassiz), and on the affinities of the Enteropneusta. Proceedings of the Royal Society of London 38:23–30.

Beckly, A. J., & Jörg Maletz. 1991. The Ordovician graptolites *Azygograptus* and *Jishougraptus* in Scandinavia and Britain. Palaeontology 34:887–925.

Bond, D. P. G., & S. E. Grasby. 2020. Late Ordovician mass extinction caused by volcanism, warming, and anoxia, not cooling and glaciation. Geology 48: 777–781.

Bouček, Bedřich. 1933. Monographie der obersilurischen Graptolithen aus der Familie Cyrtograptidae. Práce geologicko-paleontologického ústavu Karlovy university v Praze 1:1–84, 7 pl.

Bouček, Bedřich. 1957. The dendroid graptolites of the Silurian of Bohemia. Rozpravy Ustredniho ustavu Geologickeho 23:1–294, pl. 1–39.

Bouček, Bedřich, Milena Mihajlovic, & Miroslav Veselinovic. 1976. Graptolites of Upper Silurian and Lower Devonian of Zvonačka Banja (Eastern Yugoslavia). Classe de l'Académie serbe des sciences et des arts, Classe des sciences mathematiques et naturelles 39:79–114.

Bouček, Bedřich, & Alois Přibyl. 1952. Taxonomy and phylogeny of some Ordovician graptolites. Bulletin international de l`Academie tchèque des Sciences 52(20):1–17.

Boyle, James, H. D. Sheets, Shuang-Ye Wu, Daniel Goldman, M. J. Melchin, R. A. Cooper, P. M. Sadler, & C. E. Mitchell. 2017. The impact of geographic range, sampling, ecology, and time on extinction risk in the volatile clade Graptoloida. Paleobiology 43(1):85–113.

Bulman, O. M. B. 1933. Programme evolution in the Graptolites. Biological Reviews 8:311–334.

Bulman, O. M. B. 1958. Patterns of colonial development in graptolites. Journal of the Linnean Society of London, Zoology 44:24–32.

Bulman, O. M. B. 1960. Some morphologically intermediate genera in graptolite phylogeny. International Geological Congress 21(22):63–70.

Bronn, H. G. 1835. Lethaea Geognostica, Erster Band, das Übergangs-, bis Oolithen-Gebirge enthaltend. Schweizerbart. Stuttgart. 768 p.

Cameron, C. B. 2016. *Saccoglossus testa* from the Mazon Creek Fauna (Pennsylvanian of Illinois) and the evolution of acron worms (Enteropneusta: Hemichordata). Palaeontology 49(3):329–336.

Cameron, C. B. 2018. Part V, Second Revision, Chapter 2: Class Enteropneusta: Introduction, morphology, life habits, systematic descriptions, and future research. Treatise Online 109:1–22.

Cannon, J. T., A. L. Rychel, Heather Eccleston, K. M. Halanych, & B. J. Swalla. 2009. Molecular phylogeny of Hemichordata, with updated status of deep-sea enteropneusts. Molecular Phylogenetics and Evolution 52:17–24.

Carruthers, William. 1867. On Graptolites. Appendix D. *In* R. I. Murchison, Siluria. 4th Edition. John Murray. London. p. 538–541.

Chapman, A. J., P. N. Durman, & R. B. Rickards. 1996. A provisional classification of the graptolite Order Dendroidea. Paläontologische Zeitschrift 70(1–2):189–202.

Chen Xu, Chen Qing, K. P. Aung, & L. A. Muir. 2020. Latest Ordovician graptolites from Mandalay Region, Myanmar. Palaeoworld 29:47–65.

Chen Xu, Fan Jun Xuan, M. J. Melchin, & C. E. Mitchell. 2005. Hirnantian (latest Ordovician) graptolites from the Upper Yangtze region, China. Palaeontology 48:235–280.

Chen Xu, & Lin Yaokun. 1978. Lower Silurian graptolites from Tongzi, northern Guizhou. Memoir of the Nanjing Institute of Geology and Palaeontology, Academia Sinica 12:1–106, 19 pl. In Chinese, with English summary.

Chen Xu, M. J. Melchin, Fan Junxuan, & C. E. Mitchell. 2003. Ashgillian graptolite fauna of the Yangtze region and the biogeographical distribution of diversity in the latest Ordovician. Bulletin de la Societé géologique de France 174(2):141–148.

Chen Xu, M. J. Melchin, H. D. Sheets, C. E. Mitchell, & Fan Junxuan. 2005. Patterns and processes of latest Ordovician graptolite extinction and recovery based on the data from South China. Journal of Paleontology 79:842–861.

Chen Xu, Zhang Yuandong, Yu Guohua, & Liu Xiao. 2007. Latest Ordovician and earliest Silurian graptolites from northwestern Zhejiang, China. Acta Palaeontologica Sinica 46(supplement):77–82.

Cooper, R. A., & R. A. Fortey. 1982. The Ordovician graptolites of Spitsbergen. Bulletin of the British Museum (Natural History), Geology Series 36(3):157–302.

Cooper, R. A., & P. M. Sadler. 2010. Facies preference predicts extinction risk in Ordovician graptolites. Paleobiology 36(2):167–187.

Cooper, R. A., P. M. Sadler, Axel Munnecke, & J. S. Crampon. 2014. Graptoloid evolutionary rates track Ordovician-Silurian global climate change. Geological Magazine 151(2):349–364.

Crampton, J. S., R. A. Cooper, Michael Foote, & P. M. Sadler. 2020. Ephemeral species in the fossil record? Synchronous coupling of macroevolutionary dynamics in mid-Paleozoic zooplankton. Paleobiology 46(1):123–135.

Crampton, J. S., R. A. Cooper, P. M. Sadler, & Michael Foote. 2016. Greenhouse-icehouse transition in the late Ordovician marks a step change in extinction regime in the marine plankton. Proceedings of the National Acadeny of Sciences 113(6):1498–1503.

Crampton, J. S., S. R. Meyers, R. A. Cooper, P. M. Sadler, Michael Foote, & David Harte. 2018. Pacing the Paleozoic macroevolutionary rates by Milankovitch cycles. Proceedings of the National Acadeny of Sciences 115(22):5686–5691.

Eisel, Robert. 1912. Über zonenweise Entwicklung der Rastriten und Demirastriten. Jahresbericht der Gesellschaft von Freunden der Naturwissenschaften Gera 53–54:27–43, 3 pl. [different pagination in reprint, 1–17, 3 pl.].

Elles, G. L. 1898. The graptolite fauna of the Skiddaw Slates. Quarterly Journal of the Geological Society 54:463–539

Elles, G. L. 1922. The graptolite faunas of the British Isles. A study in evolution. Proceedings of the Geologist's Association 33(3):168–200.

Erdtmann, B.-D. 1982. A reorganisation and proposed phylogenetic classification of planktic Tremadoc (early Ordovician) dendroid graptolites. Norsk Geologisk Tiddskrift 62:121–144.

Fang Y.-T., Liangsi J. I., Zhang D.-L., & Yu J.-L. 1990. Stratigraphy and graptolite fauna of Lishuwo Formation from Wuning, Jiangxi. Nanjing University Publishing House. Nanjing. 155 p. In Chinese, with English summary.

Finnegan Seth, Kristin Bergmann, J. M. Eiler, D. S. Jones, D. A. Fike, Ian Eisenman, N. C. Hughes, A. K. Tripati, & W. W. Fischer. 2011. The magnitude and duration of Late Ordovician-Early Silurian glaciation. Science 331:903–906.

Finney, S. C. 1985. Nemagraptid graptolites from the Middle Ordovician Athens Shale, Alabama. Journal of Paleontology 59(5):1100–1137.

Flessa, K. W., & David Jablonski. 1983. Extinction is here to stay. Paleobiology 9(4):315–321.

Foote, Michael, P. M. Sadler, R. A. Cooper, & J. S. Crampton. 2019. Completeness of the known graptoloid palaeontological record. Journal of the Geological Society, London 176:1038–1055.

Fortey, R. A., & R. A. Cooper. 1986. A phylogenetic classification of the graptoloids. Palaeontology 29(4):631–654.

Fortey, R. A., Zhang Yuandong, & Claire Mellish. 2005. The relationships of biserial graptolites. Palaeontology 48(6):1241–1272.

Frech, Fritz. 1897. Lethaea Geognostica 1. Lethaea Palaeozoica 1, 11, Graptolithen. Stuttgart. 690 p.

Goldman, Daniel, S. M. Bergström, & C. E. Mitchell. 1995. Revision of the zone 13 graptolite biostratigraphy in the Marathon, Texas, standard succession and its bearing on Upper Ordovician graptolite biogeography. Lethaia 28:115–128.

Goldman, Daniel, Jörg Maletz, M. J. Melchin, & Fan Junxuan. 2013. Chapter 26. Graptolite palaeobiogeography. Geological Society, London, Memoirs 38:415–428.

Goldman, Daniel, C. E. Mitchell, M. J. Melchin, Fan Jun Xuan, & Wu S.-Y. 2011. Biogeography and mass extinction: extirpation and re-invasion of *Normalograptus* species (Graptolithina) in the Late Ordovician palaeo-tropics. Proceedings of the Yorkshire Geology Society 58:227–246.

Halanych, K. M. 1995. The phylogenetic position of the pterobranch hemichordates based on 18S rDNA sequence data. Molecular Phylogenetics and Evolution 4:72–76.

Hall, James. 1858. Note upon the genus Graptolithus, and description of some remarkable new forms from the shales of the Hudson River Group, discovered in the investigations of the Geological Survey of Canada, under the direction of Sir W. E. Logan, F.R.S. Canadian Naturalist and Quarterly Journal of Science 3, 139–150, 161–177. [also: Hall, James. 1858. Report [on Canadian graptolites]. Progress Report—Geological Survey of Canada 109–145. (extracted from Sir William E. Logan's Report of Progress for 1857) (pagination 1–39 in author's copy). John Lovell, Montreal].

Hall, James. 1865. Figures and descriptions of Canadian organic remains. Decade II, Graptolites of the Quebec Group. Geological Survey of Canada. A. B. Dawson Brothers. Montreal. 154 p.

Harkness, Robert. 1851. Descriptions of the graptolites found in the black shales of Dumfriesshire. Quarterly Journal of the Geological Society 7:58–65.

Hennig, Willi. 1950. Grundzüge einer Theorie der phylogenetischen Systematik. Deutscher Zentral-Verlag. Berlin. 370 p.

Hennig, Willi. 1965. Phylogenetic Systematics. Annual Review of Entomology 10:97–116.

Hennig, Willi. 1999. Phylogenetic Systematics. University of Illinois Press. Urbana & Chicago. 2263 p.

Hopkinson, John. 1869. On British graptolites. Journal of the Quekett Microscopical Club 1:151–166.

Hundt, Rudolf. 1935. Die Graptolithenfauna des obersten Obersilurs Thüringens (mit einem Beitrag über Graptolithen in Roteisensteinknollen). Zeitschrift für Naturwissenschaften 91(1):1–34.

Hutt, J. E. 1974. A new group of Llandovery biform monograptids. Special Papers in Palaeontology 13: 189–203.

Jaanusson, Valdar. 1973. Morphological discontinuities in the evolution of graptolite colonies. *In* R. S. Boardsman, A. H. Cheetham, & W. A. Oliver, Jr., eds., Animal Colonies. Development and Function through Time. Dowden, Hutchinson & Ross. Stroudsburg. p. 515–521.

Jaeger, Hermann. 1959. Graptolithen und Stratigraphie des jüngsten Thüringer Silurs. Abhandlungen der deutschen Akademie der Wissenschaften zu Berlin, Klasse für Chemie, Geologie und Biologie 1959(2):1–197.

Jaeger, Hermann. 1978. Entwicklungszüge [Trends] in der Evolution der Graptolithen. Schriftenreihe für geologische Wissenschaften 10:5–58.

Jaeger, Hermann. 1991. Neue Standard-Graptolithenzonenfolge nach der "Großen Krise" an der Wenlock/Ludlow-Grenze (Silur). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 182(3):303–354.

Jaekel, Otto. 1889. Über das Alter des sog. Graptolithengesteins mit besonderer Berücksichtigung der in demselben enthaltenen Graptolithen. Zeitschrift der deutschen geologischen Gesellschaft 41:653–716.

Koren', T. N. 1979. Late monograptid faunas and the problem of graptolite extinction. Acta Palaeontologica Polonica 24:79–106.

Koren', T. N. 1987. Graptolite dynamics in Silurian and Devonian time. Bulletin of the Geological Society of Denmark 35:149–159.

Koren', T. N. 1991. Evolutionary crisis of the Ashgill graptolites. Geological Survey of Canada, Paper 90–9:157–164.

Koren', T. N., & A. A. Sujarkova. 2004. The Ludlow (Late Silurian) neocucullograptid fauna from the southern Tien Shan, Kyrghizstan. Alcheringa 28(2):333–387.

Kozłowski, Roman. 1954. O budowie nietorych Dichograptidae (Sur la structure de certain dichograptidés). Acta Geologica Polonica 4:423–444. French translation, 118–135.

Lankester, E. R. 1870. On the Use of the Term Homology in Modern Zoology, and the Distinction between Homogenetic and Homoplastic Agreements. The Annals and Magazine of Natural History, Zoology, Botany, and Geology 4(6):34–43.

Lapworth, Charles. 1876. On Scottish Monograptidae (continued from page 321). Geological Magazine 13:350–360.

Lee, C. K. 1961. Graptolites from the Dawan Formation (Lower Ordovician) of W. Hupeh and S. Kueichou. Acta Palaeontologica Sinica 9:48–79.

Legrand, Philippe. 2001. La faune graptolitique de la region d'in Azaoua (Tassili Oua-N-Ahaggar, confins Algero-Nigeriens). Annales de la Societé Géologique du Nord 8(2):137–158.

Legrand, Philippe. 2009. Faunal specificity, endemism and paleobiogeography: the post-glacial (Hirnantian-early Rhuddanian) graptolite fauna of the North-African border of Gondwana: A case study. Bulletin de la Societé géologique de France 180(4):353–367.

Lenz, A. C., D. E. B. Bates, Anna Kozłowska, & Jörg Maletz. 2018. Part V, Revision 2, Chapter 26: Family Retiolitidae: Introduction and taxonomy. Treatise Online 114:1–37.

Lenz, A. C., & M. J. Melchin. 2008. Convergent evolution in two Silurian graptolites. Acta Palaeontologica Polonica 53(3):449–460.

Lenz, A. C., P. J. Noble, Monika Masiak, S. R. Poulson, & Anna Kozłowska. 2006. The lundgreni Extinction Event: integration of paleontological and geochemical data from Arctic Canada. GFF 128(2):153–158.

Lenz, A. C., Sherill Senior, Anna Kozłowska, & M. J. Melchin. 2012. Graptolites from the mid Wenlock (Silurian), Middle and Upper Sheinwoodian, Arctic Canada. Palaeontographica Canadiana 32:1–93.

Lindholm, Kristina.1991. Ordovician graptolites from the early Hunneberg of southern Scandinavia. Palaeontology 34(2):283–327.

Linnæus, Carolus. 1735. Systema naturæ, sive regna tria naturæ systematice proposita per classes, ordines, genera, and species. Lugduni Batavorum. (Haak). p. 1–12 [http://www.biodiversitylibrary.org/item/15373].

Linnæus, Carolus. 1758. Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. p. [1–4], 1–824. Holmiæ. (Salvius) [http://reader.digitale-sammlungen.de/resolve/display/bsb10076014.html; http://www.biodiversitylibrary.org/item/10277].

Loydell, D. K. 1993. Upper Aeronian and Lower Telychian (Llandovery) graptolites from western Mid-Wales, Part 2. Monograph of the Palaeontographical Society 147 (592):56–180.

Lukasik, J. J., & M. J. Melchin. 1997. Morphology and classification of some early Silurian monograptids (Graptoloidea) from the Cape Phillips Formation, Canadian Arctic Islands. Canadian Journal of Earth Sciences 34(8):1128–1149.

Maletz, Jörg. 1994. The rhabdosome architecture of *Pterograptus* (Graptoloidea, Dichograptidae). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 191:345–356.

Maletz, Jörg. 2010a. *Xiphograptus* and the evolution of the virgella-bearing graptoloids. Palaeontology 53(2):415–439.

Maletz, Jörg. 2010b. Retiolitid graptolites from the collection of Hermann Jaeger II: *Cometograptus, Spinograptus* and *Plectograptus*. Paläontologische Zeitschrift 84:501–522.

Maletz, Jörg. 2014. Hemichordata (Pterobranchia, Enteropneusta) and the fossil record. Palaeogeography, Palaeoclimatology, Palaeoecology 398:16–27.

Maletz, Jörg. 2017a. Graptolite Paleobiology. Topics in Palaeobiology. (Mike Benton, Series ed.,). Wiley-Blackwell. Chichester. 323 p., 16 pl.

Maletz, Jörg. 2017b. Fossils explained 70. Graptolites: fossil and living. Geology Today 33(6):237–244.

Maletz, Jörg. 2018. Part V, Second revision, Chapter 5: Hemichordate taphonomy. Treatise Online 110:1–15.

Maletz, Jörg. 2019. Tracing the evolutionary origins of the Hemichordata (Enteropneusta & Pterobranchia). Palaeoworld 28:58–72.

Maletz, Jörg. 2020a. Hemichordata (Enteropneusta & Pterobranchia, incl. Graptolithina): A review of their fossil preservation as organic material. Bulletin of Geosiences 95:(1)41–80 [doi.10.3140/bull.geosci.1776].

Maletz, Jörg. 2020b. Part V, Second Revision, Chapter 23: Suborder Axonophora, infraorder Diplograptina 2 (Climacograptidae, Dicranograptidae): Introduction, morphology, and systematic descriptions. Treatise Online 129:1–20.

Maletz, Jörg. 2020c. Part V, Second Revision, Chapter 8: Paleogeography of the Hemichordata. Treatise Online 133:1–12.

Maletz, Jörg, Jesse Carlucci, & C. E. Mitchell. 2009. Graptoloid cladistics, taxonomy & phylogeny. Bulletin of Geosciences 84:7–19.

Maletz, Jörg, M. J. Melchin, Peter Bullock, T. N. Koren', & Jennifer Russel-Houston. 2019. *Paramonoclimacis sidjachenkoi* (Obut & Sobolevskaya, 1968) and the origin of the streptograptid thecal aperture. Papers in Palaeontology 5(3):499–520.

Maletz, Jörg, Zhang Yuandong, & A. H. M. VandenBerg. 2018. Part V, Second Revision, Chapter 19: Suborder Sinograptina: Introduction, morphology, and systematic descriptions. Treatise Online 107:1–23.

Melchin, M. J. 1998. Morphology and phylogeny of some early Silurian 'diplograptid' genera from Cornwallis Island, Arctic Canada. Palaeontology 41(2):263–315.

Melchin, M. J., A. C. Lenz, & Anna Kozłowska. 2017. Retiolitine graptolites from the Aeronian and lower Telychian (Llandovery, Silurian) of Arctic Canada. Journal of Paleontology 91(1):116–145.

Melchin, M. J., & C. E. Mitchell. 1991. Late Ordovician extinction in the Graptoloidea. Geological Survey of Canada Paper 90–9:143–156.

Melchin, M. J., C. E. Mitchell, Amanda Naczak-Cameron, Fan, Jun Xuan, & Jason Loxton. 2011. Phylogeny and adaptive radiation of the Neograpina (Graptoloidea) during the Hirnantian mass extinction and Silurian recovery. Proceedings of the Yorkshire Geological Society 58(4):281–309.

Mitchell, C. E. 1987. Evolution and phylogenetic classification of the Diplograptacea. Palaeontology 30(2):353–405.

Mitchell, C. E. 1990. Directional macroevolution of the diplograptacean graptolites: A product of astogenetic heterochrony and directed speciation. *In* P. D. Taylor & G. P. Larwood, eds., Major Evolutionary Radiations. Clarendon Press. Oxford Systematics Association Special Volume 42:235–264.

Mitchell, C. E., M. J. Melchin, C. B. Cameron, & Jörg Maletz. 2013. Phylogenetic analysis reveals that *Rhabdopleura* is an extant graptolite. Lethaia 46:34–56.

Mu Enzhi, Li Jijin, Ge Meiyu, Chen Xu, Lin Yaokun, & Ni Yunan. 1993. Upper Ordovician graptolites of central China region. Palaeontologia Sinica, New Series B 182(29):1–393, 66 pl.

Mu Enzhi, & Ni Yunan. 1983. Uppermost Ordovician and Lowermost Silurian graptolites from the Xainza area of Xizang (Tibet) with discussion on the Ordovician-Silurian boundary. Palaeontologica Cathayana 1:151–179.

Murchison, R. I. 1867. Siluria. 4th Edition. John Murray. London. p. 566. [Includes William Carruthers. On Graptolites. Appendix D. p. 538–541.]

Nanglu, Karma, J.-B. Caron, Simon Conway Morris, & C. B. Cameron. 2016. Cambrian suspension-feeding tubicolous enteropneusts. BMC Biology 14(56):1–9.

Ni Yu-nan. 1978. Lower Silurian graptolites from Yichang, western Hubei. Acta Palaeontologica Sinica 17:387–416. In Chinese, with English summary.

Nicholson, H. A. 1867. On some fossils from the Lower Silurian rocks of the south of Scotland. Geological Magazine 1(4):107–113.

Nicholson, H. A. 1868. On the nature and zoological position of the Graptolitidae. Annals and Magazine of Natural History 4(1):55–60, pl. 3.

Nicholson, H. A. 1875. On a new genus and some new species of graptolites from the Skiddaw Slates. Annales and Magazine of Natural Natural History, (series 4) (16):269–273.

Nicholson, H. A. & J. E. Marr. 1895. Notes on the phylogeny of the graptolites. Geological Magazine 4(2):529–539.

Obut, A. M. 1987. *Cochlograptus:* A new genus of the Silurian graptolites. Trudy Instituta Geologii i Geofiziki (Novosibirsk) 388:140–145, pl. 125. In Russian.

Obut, A. M., & R. F. Sobolevskaya. 1966. Graptolitit rannego silura i Kazachstane. Akademii Nauk SSSR, Sibirskoe Otdelenie Institut Geologii Geofiziki, Ministerstvo Geologii SSSR, Nauchno-issledovatelskie Institut Geologii Arktiki 1–56. In Russian.

Obut, A. M., R. F. Sobolevskaya, & V. I. Bondarev. 1965. Silurian graptolites of Taimyr. Akademiya Nauk SSSR, Moscow. 120 p. In Russian.

Obut, A. M., R. F. Sobolevskaya, & A. P. Merkureva. 1968. Graptolity llandoveri v kernakh burovykh skvazhin Noril'skogo rayona. Nauka. Moscow. 137 p. In Russian.

Philippe, Hervé, Henner Brinkmann, R. R. Copley, L. L. Moroz, Hiroaki Nakano, A. J. Poustka, Andreas Wallberg, K. J. Peterson, & M. J. Telford. 2011. Acoelomorph flatworms are deuterostomes related to *Xenoturbella*. Nature 470:255–260.

Přibyl, Alois. 1941. *Pernerograptus* nov. gen. a jeho zástupci z českého a cizího siluru. [*Pernerograptus* nov. gen. und seine Vertreter aus dem böhmischen und ausländischen Silur]. Věstník Královské České Společnosti Nauk. Třída Matemat.-Přirodověd. Rocnik 1941:1–19. Czech text: 1–7, 15–18; German text: 8–14.

Přibyl, Alois. 1967. *Monograptus* (*Testograptus*) subgen. nov. aus dem böhmischen und europäischen Silur. Ustredni Ustav Geologicky Vestnik 42(1):49–52.

Rickards, R. B. 1977. Chapter 10. Patterns of evolution in the graptolites. Developments in Palaeontology and Stratigraphy 5:333–358.

Rickards, R. B., J. E. Hutt, & W. B. N. Berry. 1977. Evolution of Silurian and Devonian graptoloids. Bulletin of the British Museum of Natural History, Geological Series 28(1):1–120.

Rickards, R. B., G. H. Packham, A. J. Wright, & P. L. Williamson. 1995. Wenlock and Ludlow graptolite faunas and biostratigraphy of the Quarry Creek district, New South Wales. Memoir of the Association of Australasian Palaeontologists 17:1–68.

Rickards, R. B., & A. J. Wright. 2002. Lazarus taxa, refugia and relict faunas: Evidence from graptolites. Journal of the Geological Society, London 159:1–4.

Rigby, Susan, & Claire Milsom. 1996. Benthic origins of zooplankton: An environmentally determined macroevolutionary effect. Geology 24(1):52–54.

Sadler, P. M., R. A. Cooper, & M. J. Melchin. 2011. Sequencing the graptoloid clade: Building a global diversity curve from local range charts, regional composites and global time-lines. Proceedings of the Yorkshire Geological Society 58:329–343.

Salter, J. W. 1863. Note on the Skiddaw Slate Fossils. Quarterly Journal of the Geological Society of London 19:135–140.

Sheets, H. D., C. E. Mitchell, M. J. Melchin, Jason Loxton, Petr Štorch, K. L. Carlucci, & A. D. Hawkins. 2016 Graptolite community responses to global climate change and the late Ordovician mass extinction. Proceedings of the National Academy of Sciences 113:8380–8385.

Skevington, David. 1966. The morphology and systematics of "*Didymograptus*" *fasciculatus* Nicholson, 1869. Geological Magazine 103(6):487–497.

Skevington, David. 1967. Probable instance of genetic polymorphism in the graptolites. Nature 213 (5078):810–812.

Skwarko, S. K. 1974. Some graptolites from the Canning Basin, Western Australia 2. Graptolites from the Goldwyer No. 1 well. Bulletin of the Bureau of Mineral Resources, Geology and Geophysics of Australia 150:43–56.

Sobolevskaya, R. F. 1974. New Ashgill graptolites in the middle flow basin of the Kolyma-River. *In* O. T. Obut, ed., Graptolites of the USSR. Nauka, Siberian Branch, Novosibirsk**.** p. 63–71. In Russian.

Štorch, Petr. 1995. Biotic crises and post-crisis recoveries recorded by Silurian planktonic graptolite faunas of the Barrandian area (Czech Republic). Geolines 3:59–70.

Štorch, Petr, & M. J. Melchin. 2019. Lower Aeronian triangulate monograptids of the genus *Demirastrites* Eisel, 1912: biostratigraphy, palaeobiogeography, anagenetic changes and speciation. Bulletin of Geosciences 93(4):513–537.

Štorch, Petr, C. E. Mitchell, S. C. Finney, & M. J. Melchin. 2011. Uppermost Ordovician (upper Katian–Hirnantian) graptolites of north-central Nevada, U.S.A. Bulletin of Geosciences 86(2):301–386.

Strachan, Isles. 1952. On the development of *Diversograptus* Manck. Geological Magazine 89(5):365–368.

Sudbury, Margaret. 1958. Triangulate Monograptids from the *Monograptus gregarius* zone (Lower Llandovery) of the Rheidol Gorge (Cardiganshire). Philosophical Transactions of the Royal Society of London, Series B. Geological Sciences 241(685):485–555.

Suess, E. 1851. Über böhmische Graptolithen. Naturwissenschaftliche Abhandlungen von W. Haidinger 4:87–134.

Teller, Lech. 1976. Morphology of some Upper Wenlockian Cyrtograptinae from Zawada 1 profile (NE Poland). Acta Geologica Polonica 26(4):469–484.

Thorsteinsson, Raymond.1955. The mode of cladial generation in *Cyrtograptus*. Geological Magazine 92(1):37–49.

Törnquist, S. V. 1904. Researches into the Graptolites of the Lower Zones of the Scanian and Vestrogothian Phyllo-Tetragraptus beds 2. Lunds Universitets Årsskrift 40, Afdeln. 2(2):1–29, 4 pl. Also Kongliga Fysiografiska Sallskapets Handlingar 15(2):1–29, 4 pl.

Tsegelnjuk, P. D. 1976. Late Silurian and early Devonian monograptids from the south-western margin of the East European Platform (in Russian). *In* P. L. Shulga, ed., Palaeontology and Stratigraphy of the Upper Precambrian and Lower Paleozoic of the South-West Part of the East European Platform. Naukova Dumka. Kiev. p. 91–133.

Tullberg, S. A. 1880. Tvenne nya Graptolitslägten. Geologiska Föreningens i Stockholm Förhandlingar 5(7):313–315.

Urbanek, Adam. 1960. An attempt at biological interpretation of evolutionary changes in graptolite colonies. Acta Palaeontologica Polonica 5(2):127–234.

Urbanek, Adam. 1963. On generation and regeneration of cladia in some Upper Silurian monograptids. Acta Palaeontologica Polonica 8(2):135–254.

Urbanek, Adam. 1966. On the morphology and evolution of the Cucullograptinae (Monograptidae, Graptolithina). Acta Palaeontologica Polonica 11(3–4):291–544.

Urbanek, Adam. 1970. Neocucullograptinae n. subfam. (Graptolithina) their evolutionary and stratigraphic bearing. Acta Palaeontologica Polonica 15(2–3):163–388.

Urbanek, Adam. 1987. The phylogenetic debate on the affinities of graptolites. An attempt at a methodological analysis. Bulletin of the Geological Society of Denmark 35:223–230.

Urbanek, Adam. 1993. Biotic crises in the history of Upper Silurian graptoloids: A palaeobiological model. Historical Biology 7:29–50.

Urbanek, Adam. 1995. Phyletic evolution of the latest Ludlow spinose monograptids. Acta Palaeontologica Polonica 40(1):1–17.

Urbanek, Adam. 1997. Late Ludfordian and early Pridoli monograptids from the Polish Lowland. Palaeontologia Polonica 56:87–232.

Urbanek, Adam. 1998. Oligophyly and evolutionary parallelism: A case study of Silurian graptolites. Acta Palaeontologica Polonica 43(4):549–572.

Urbanek, Adam, Sigitas Radzevičius, Anna Kozłowska, & Lech Teller. 2012. Phyletic evolution and iterative speciation in the persistent *Pristiograptus dubius* lineage. Acta Palaeontologica Polonica 57(3):589–611.

VandenBerg, A. H. M. 2017. Revision of zonal and related graptolites of the topmost Lancefieldian and Bendigonian (early Floian) graptolite sequence of Victoria, Australia. Proceedings of the Royal Society of Victoria 129:39–74.

Whittingham, Misha, Sigitas Radzevičius, & Andrej Spiridonov. 2020. Moving towards a better understanding of iterative evolution: An example from the late Silurian Monograptidae (Graptolithina) of the Baltic Basin. Palaeontology 63(4):629–649.

Wignall, P. B., & M. J. Benton. 1999. Lazarus taxa and fossil abundance at times of biotic crisis. Journal of the Geological Society, London 156:453–456.

Williams, S. H., & R. K. Stevens. 1988. Early Ordovician (Arenig) graptolites from the Cow Head Group, western Newfoundland. Palaeontographica Canadiana 5:1–167.

Wood, E. M. R. 1900. The lower Ludlow formation and its graptolite fauna. Quarterly Journal of the Geological Society of London 56:415–492.

Xu Chen, Zhang Yuandong, Yu G. H., & Liu Xiao. 2007. Latest Ordovician and earliest Silurian graptolites form North-western Zhejiang, China. Acta Palaeontologica Sinica 46(supplement):77–82.

Zalasiewicz, Jan, Mark Williams, & Maxine Akhurst. 2003. An unlikely evolutionary lineage: the Rhuddanian (Silurian, Llandovery) graptolites *Huttagraptus*? *praematurus* and *Coronograptus cyphus* re-examined. Scottish Journal of Geology 39(1):89–96.